Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Climate, landscape, habitat, and woodland management associations with hazel dormouse *Muscardinus avellanarius* population status

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Keywords
citizen science, conservation assessment, hazel dormouse, protected species, woodland management

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Submitted: 8 August 2017
Returned for revision: 9 October 2017
Revision accepted: 23 January 2018
Editor: DR

doi: 10.1111/mam.12125

ABSTRACT

1. Although strictly protected, populations of the hazel dormouse *Muscardinus avellanarius* in the UK declined by 72% from 1993 to 2014. Using National Dormouse Monitoring Programme data from 300 sites throughout England and Wales, we investigated variation in hazel dormouse population status (expressed as Indices of Abundance, Breeding, and population Trend) in relation to climate, landscape, habitat, and woodland management.
2. Dormice were more abundant and produced more litters on sites with warmer, sunnier springs, summers, and autumns. Dormouse abundance was also higher on sites with consistently cold local climate in winter. Habitat connectivity, woodland species composition, and active site management were all correlated with greater dormouse abundance and breeding. Abundances were also higher on sites with successional habitats, whereas the abundance of early successional bramble *Rubus fruticosus* habitat, woodland area, and landscape connectivity were important for population stability.
3. Diversity in the structure of woodlands in Europe has decreased over the last 100 years, and the habitats we found to be associated with more favourable dormouse status have also been in decline. The conservation status

of the hazel dormouse, and that of woodland birds and butterflies, may benefit from reinstatement or increased frequency of management practices, such as coppicing and glade management, that maintain successional and diverse habitats within woodland.

INTRODUCTION

Critical appraisal of the environmental variables that affect the status of threatened species can help determine the relative influence of factors that might more easily be modified, such as habitat and management, alongside those that cannot, such as climate (Pressey et al. 2007, Groves et al. 2012). Furthermore, understanding the drivers of variation in status at different spatial scales can allow the identification of regions that offer the best conservation opportunities, as well as the distinguishing characteristics of sites that offer high habitat quality, even when favourable location is accounted for (Erasmus et al. 1999, Chalfoun & Martin 2007). Such assessments are especially pressing for vulnerable or protected species facing multiple threats, and where legislation makes action to conserve them a legal imperative (Koleček et al. 2014, Sanderson et al. 2016).

The hazel dormouse *Muscardinus avellanarius* is a European Protected Species, listed under Annex IV of the European Commission Habitats Directive (1992), and the UK Habitats Regulations (1994 and 2010). The species is categorised on the International Union for Conservation of Nature (IUCN) Red List as Least Concern. At the edges of its range, such as in the United Kingdom, the species is in decline (Hutterer et al. 2016) and a recent, robust analysis of dormouse counts from 400 sites throughout the species' range in England and Wales revealed a 72% (95% confidence intervals: 62–79%) decline in the UK dormouse population from 1993 to 2014 (Goodwin et al. 2017). This decline, together with evidence of range contraction (Bright & Morris 1996) substantiates a Red List categorisation of the hazel dormouse as Vulnerable or possibly Endangered in the UK (Goodwin et al. 2017). Dormouse declines are particularly concerning given their strict protection and the significant monitoring and conservation attention this species has received over recent decades (White 2012). Understanding the needs of threatened species and whether legislative instruments are serving as effective tools in their conservation are therefore both vital in developing effective policy and practice (Pärtel et al. 2005, Ramirez et al. 2017).

In areas where dormice numbers appear to be in decline, proposed causes have included habitat loss, habitat fragmentation, and declining habitat quality (Bright & Morris 1996, Mortelliti et al. 2011, Reiners et al. 2012, Amici et al. 2015). Recent climate change may also have contributed to dormouse declines, especially at the edges of its range. Milder, more variable winter conditions have been linked to higher over-winter mortality, and wetter spring and summer weather may have negatively impacted populations through reductions in activity and in the availability of food (Bright & Morris 1996, Juškaitis 1999, Juškaitis et al. 2016). At a larger scale, changes in landscape structure, primarily via agricultural intensification, have led to increased fragmentation of woodland habitats and the loss of semi-natural vegetation (Peterken 2002, Hopkins & Kirby 2007), reducing habitat availability for dormice and compromising their ability to disperse among woodlands (Bright & Morris 1996, Mortelliti et al. 2011).

There have been significant shifts in the habitat characteristics of European temperate forests over the last century, including the intensification of timber production and abandonment of traditional broadleaf management practices, such as coppicing and creation of glades and rides (Young et al. 2005, Miklín & Čížek 2014, Kirby et al. 2017). This has resulted in a predominance of two broad woodland types: intensively managed commercial conifer plantations and mature, broadleaf high-forest (Paillet et al. 2010). This trend is particularly apparent in the UK, where the simultaneous intensification of forestry and abandonment of traditional woodland management has led to a reduction in the abundance and distribution of structurally complex and spatially heterogeneous woodland (Hopkins & Kirby 2007, Quine et al. 2011). Shifts in the ecological communities of woodlands, notably increasing deer population densities, have further reduced structural complexity, with negative consequences for biodiversity (Eichhorn et al. 2017). Heterogeneous, multi-layered woodland brings biodiversity benefits (Lindenmayer et al. 2006, Kirby et al. 2017) by providing important habitats for a range of key taxa such as butterflies and moths (Broome et al. 2011, Fartmann et al. 2013, Fox 2013), woodland birds (Fuller & Gill 2001, Fuller et al. 2007, Quine et al. 2007), and mammals (Ramírez & Simonetti 2011).

Hazel dormice have been associated with early- to mid-successional wooded habitats that often arise from traditional management regimes, such as coppicing and ride and glade maintenance (Capizzi et al. 2002, Sozio et al. 2016). However, studies of the effects of habitat variation and management interventions on dormice have been focused on few sites or have taken place for limited periods, due to the logistical difficulties of examining multiple

sites over appropriate time-scales (Juškaitis 2008, Trout et al. 2012, Sozio et al. 2016). The National Dormouse Monitoring Programme (NDMP) consists of nest box recording undertaken by volunteers on a large sample of sites throughout England and Wales. It has been running since 1988, and by 2017 it had encompassed over 600 sites. The spatial and temporal scale of the NDMP therefore allows for assessment of populations across different habitat, landscape, and climate contexts. Sampling effort (the number of nest boxes) is known, and NDMP count data have been shown to provide reliable indices of relative abundance that are robust to the variation in survey implementation that is intrinsic to such citizen science schemes, including changes in effort over time and on sites surveyed in different months or for different numbers of years (Goodwin et al. 2017). In this study, we have used NDMP data to assess the climatic, landscape, habitat, and management correlates of hazel dormouse abundance, breeding, and population trends, with a view to understanding and countering dormouse population declines.

METHODS

Dormouse population data

Grids of dormouse nest boxes are established on NDMP sites throughout England and Wales, and dormice are counted by licensed volunteers up to once a month from May to September, with at least one pre-breeding survey in May/June and one post-breeding survey in September/October. Detailed survey methodology is provided in the NDMP guidelines (Anonymous 2016a) and details of the validation of NDMP data for population monitoring are provided by Goodwin et al. (2017). Sites have been monitored for 1–27 years and each contains 10–500 nest boxes. Data from the first 5 years of the programme (1988–1992) were excluded to prevent year effects being confounded with site effects arising from small numbers of survey sites ($n < 30$). Population indices were calculated using data from 300 sites that had been surveyed for at least 5 years during the period from 1993 to 2014, and on which more than one adult dormouse had been found. It is possible to measure change over time on sites surveyed for 5 years or more, and using only sites where dormice had been found means that indices represent relative population measures that can be compared among sites. To examine relationships with seasonal climatic variables, dormouse counts from all months of the survey season were used.

Weather and climate data

Monthly climate data were obtained from the UK Met Office, gridded at 5 × 5 km horizontal resolution. Location-specific climate estimates were derived from the grids via Inverse Distance Weighting, using the centre-points of the nearest nine grid squares. As temperature variables (minimum, mean, and maximum) and rainfall variables (total monthly rainfall and number of days with >10 mm rainfall) were closely related, one temperature and one rainfall variable, which best explained variation in dormouse indices (models with lowest Akaike Information Criterion), were selected for each season (Appendix S1: Table S1.1). Each weather variable was centred (mean-subtracted) and scaled (divided by the standard deviation) across all sites and averaged for each site across all years, giving an average value describing the climate of each site relative to other sites. Sun, rain, and temperature site averages often remained closely correlated and so we conducted Principal Component Analyses to capture variance in climate on sites (Appendix S1: Table S1.2). In analysing climate-related variation, we wanted to examine both the major axes of climatic variation, using the first Principal Components (PCs), as well as more unusual or distinctive combinations of conditions, using PCs that explained >2% of variation. We excluded all those PCs that explained <2% of variation in the data.

Landscape and habitat data

Five data sets gathered from remote sensing were used to assess habitat, landscape, and habitat change (Appendix S1: Table S1.1): 1) the National Forest Inventory for 2011–2014 from Forestry Commission England (Anonymous 2016b) was used to classify wooded habitat areas; 2) Natural England (Spencer & Kirby 1992) provided ancient woodland cover; 3) the Countryside Survey 2007 from the Centre for Ecology and Hydrology (Brown et al. 2016) provided hedgerow length; 4) the Joint Research Centre European Commission Forest Data (EC FOREST) (Pekkarinen et al. 2009, Soille & Vogt 2009, Kempeneers et al. 2011) from 2006 provided forest type (broadleaf or conifer) and spatial type (edge, isolated, and interior); and 5) Environment Agency composite LiDAR (Light Detection and Ranging) data provided vegetation height at 1 m resolution for a subset of NDMP sites.

The total area covered by Ancient Woodland and by each EC FOREST and National Forest Inventory habitat type was summed at three scales: the area covered by the nest box scheme, the whole woodland site and the surrounding landscape within 1 km of the site perimeter, and transformed into proportions to control for variation in site size. Change in the proportions of wooded habitats in different years was used as a measure of habitat turnover at sites. As the National Forest Inventory classifies habitat broadly and detects habitat patches of 0.2 ha and larger, we used a binary measure of whether there was any change

from 2011 to 2014. For EC FOREST spatial habitat type, we quantified the amount of change in habitat types between 2000 and 2006. Habitat variables were centred (by subtracting the mean) and scaled (by dividing by the standard deviation) prior to analyses due to their very different measurement scales.

Using LiDAR data, we calculated metrics based on the canopy density and proportion of different vegetation heights for a subset of sites. Canopy density was defined as the density of vegetation height points over 4 m (Mihók et al. 2009, Scheffer et al. 2014). A sliding window average (5 m window) for canopy density was calculated across sites, and the standard deviation of this value was used to quantify variation in canopy density. As these variables were all correlated, they were converted into PCs describing different vegetation structure types on sites (Appendix S1: Table S1.2).

Management and site vegetation data

Questionnaires were sent to NDMP site monitors in 2014 and 2015 to gather data on species composition and the management regimes of sites. Monitors were asked to record the abundance of trees and shrubs on the DAFOR scale (Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent). The 11 tree and shrub species that were found on at least 50% of sites were used in analysis. Simpson's diversity index was calculated for vegetation composition on each site. Site monitors were also asked about the area covered, timing and frequency of coppicing, thinning, clearfell, ride, and glade management. Management data were converted into variables quantifying broad management differences to standardise reporting; sites were classified into those that reported management and those that did not, and the total extent of management was calculated by summing the areas subject to different management practices in each year.

Statistical analysis

All analyses were conducted within the R platform (version 3.3.2).

DORMOUSE POPULATION METRICS

To compare site characteristics to dormouse population metrics and control for between-year variation in dormouse counts, time-independent, site level Indices of dormouse Abundance, Breeding, and population Trend were derived, using the approach applied by Goodwin et al. (2017). Indices were derived through models fitted to counts of dormice or breeding events with explanatory terms for year and site, with an offset for number of nest boxes present at each site, to control for survey effort (Appendix S1). Correlation between the Trend Index and log-transformed Abundance Index was investigated using Pearson's product-moment correlation (r).

ENVIRONMENTAL AND MANAGEMENT FACTORS AND DORMOUSE POPULATIONS

Two forms of analysis were conducted on the relationship between climate, habitat, landscape, and management characteristics of sites with each of the three dormouse population Indices: Abundance, Breeding, and Trend. See Fig. S1.1 in Appendix S1 for a schematic of the analytical pathway. First, we ran a Generalised Least Squares model, using the R package nlme (Pinheiro et al. 2017), including a rational-quadratics spatial correlation function to control for the fact that some sites were closer to each other and more likely to be similar, but not to control explicitly for the locations of sites (Dormann et al. 2007). We termed this the 'proximity model'; it accounts for correlations in the similarity of nearby sites, but not explicit differences in the dormouse population status of sites in different areas. Second, we ran a 'location model', a generalised additive model, fitted using the R package mgcv (Wood 2011), and including an easting and northing smoothed interaction term to account for all variation caused by the spatial location of each site relative to other sites.

We performed these two analyses, the proximity model and the location model, to investigate the relationships between the same climate, landscape, habitat, and management variables and dormouse population metrics, as we did not want to dictate whether spatial differences in dormouse population traits were determined by the similarity of nearby populations or by their geographical location. The proximity model would show which environmental characteristics operated over broader spatial scales, up to the national level, whereas the location model would show which environmental characteristics operated on a smaller spatial scale, at the local level, as differences in dormouse populations arising from site location were controlled for. In other words, this analysis would show what made a site particularly good or bad for dormice given its location.

Dormouse Abundance and Breeding Indices were log-transformed to normalise their distribution, and all models contained a Gaussian error structure. All models included a weighting term that weighted the Abundance, Breeding, and Trend Indices by their standard error, and thus by the accuracy with which they were estimated; in the location models this was a direct weight and so was entered as 1/standard error, whereas in proximity models it was expressed as a fixed variance function and so was entered as ~standard error.

Model selection was conducted using information theoretic approaches based on comparison of Akaike Information Criterion among candidate models (Appendix S1). For both the national-level proximity model and local-level location model, a two-stage selection was conducted. First, initial exploratory analysis for four separate suites of environmental variables (climate, landscape, habitat, and management) was performed separately for dormouse Abundance, Breeding, and Trend Indices of sites. All variables that were included in initial analyses are shown in Appendix S1. Initial variables were selected using biological rationale, but a two-stage process was deemed necessary to avoid limiting the research to a limited set of pre-determined hypotheses regarding dormouse habitat preferences (van de Pol et al. 2016). Potentially important variables were identified if they had a significance of $P < 0.15$ when conditional model averaging was performed following model selection (Davies et al. 2011). Each set of potentially important variables was then combined into a second-stage comparative model for each national (proximity model) and local (location model) analysis of each population index, and model selection was performed. Interactions between explanatory variables were not explored due to uneven representation of variable combinations (Zuur et al. 2010). Full model averaging was then performed across the top model set to calculate parameter estimates and confidence intervals.

VEGETATION STRUCTURE AND DORMOUSE POPULATIONS

The relationships between vegetation structure PCs derived from LiDAR and Indices of dormouse Abundance (n = 48 sites), Breeding (n = 35 sites), and Trend (n = 46 sites) were modelled using a linear regression model with a Gaussian error structure. The sites selected for LiDAR analysis were stratified by region (as described in Fig. 1), so spatial terms were not included in this model. The relationships between the original LiDAR-derived variables and dormouse population indices were also modelled using linear regression as validation. Model selection was undertaken using the approach detailed above, and full model averaging was used to determine the effect sizes and confidence intervals.

RESULTS

The mean hazel dormouse Abundance Index was 5.2 (±0.3 SE) dormice per 100 nest boxes, mean Breeding Index was 0.6 (±0.04) litters per 100 nest boxes, and mean population Trend Index was 0.946 (±0.016), which is equivalent to a 5.4% population decrease each year. The average size of the woodland area of the sites was 1.4 km^2 (±0.1 km^2), of which an average of 0.09 km^2 (±0.004 km^2), approximately 6.4%, was monitored with nest boxes. Dormice were most abundant in the South-East of England (Fig. 1). There was no significant correlation between the dormouse Abundance and Trend Indices of sites (r = 0.1, t_{213} = 1.5, P = 0.14).

Information on all environmental characters was available for 180 sites for Abundance, 140 for Breeding and 182 for Trend Indices. The most widespread habitat type was broadleaf woodland, occurring on 99% of sites, and comprising an average of 69% (± 2%) of site area. Ancient woodland occurred on 77% of sites, and on these an average of 64% (± 2%) of site area was ancient woodland. Conifer woodland occurred on 48% of sites, and on these an average of 14% (± 2%) of site area was conifer-dominated habitat. Isolated woodland, mixed broadleaf and conifer, and shrub occurred in 69%, 39% and 36% of woodland sites respectively. Hazel *Corylus avellana* was the most common species, reported at 99% of sites. Oak *Quercus* spp., bramble, honeysuckle *Lonicera periclymenum*, ash *Fraxinus* spp. and birch *Betula pendula* were all found at >90% of sites, while willow *Salix* spp., sycamore *Acer pseudoplatanus*, conifer, sweet chestnut *Castanea sativa* and yew *Taxus baccata* were reported on between 50 and 90% of sites.

Woodland management was reported to have been conducted on 88% of sites, and information on the management practices themselves was provided for 63% of sites. At these sites, an average of 0.03 km^2 (±0.004 km^2), this equates to 12% (±2%) of the woodland area under the control of the site managers, was subject to yearly management activities. There had been habitat turnover, detected by NFI data sets (2011–2014), on 22% of sites over 4 years; however, the more fine-scale EC FOREST data sets reported change on 98% of sites over 6 years (2000–2006), with an average change in habitat of 13% (±1%).

Environmental and management factors and dormouse populations

At a national scale, in the proximity model, variation in dormouse Abundance Indices was negatively related to the first climate PC (PC1; Fig. 2), indicating that dormice were more abundant on sites characterised by a climate of warmer and sunnier springs, summers, and autumns. Local-scale analysis via the location model identified that site location was important in determining the Abundance Index of a site; 38% of variance in abundance could be explained by location alone, whereas 27% could be attributed to habitat and management factors. Site-level climatic variation explained 7% of variance in Abundance Indices and, when controlling for the location of sites, colder, less variable winter temperatures (PC3) were related to higher Abundance Indices. Dormouse Abundance

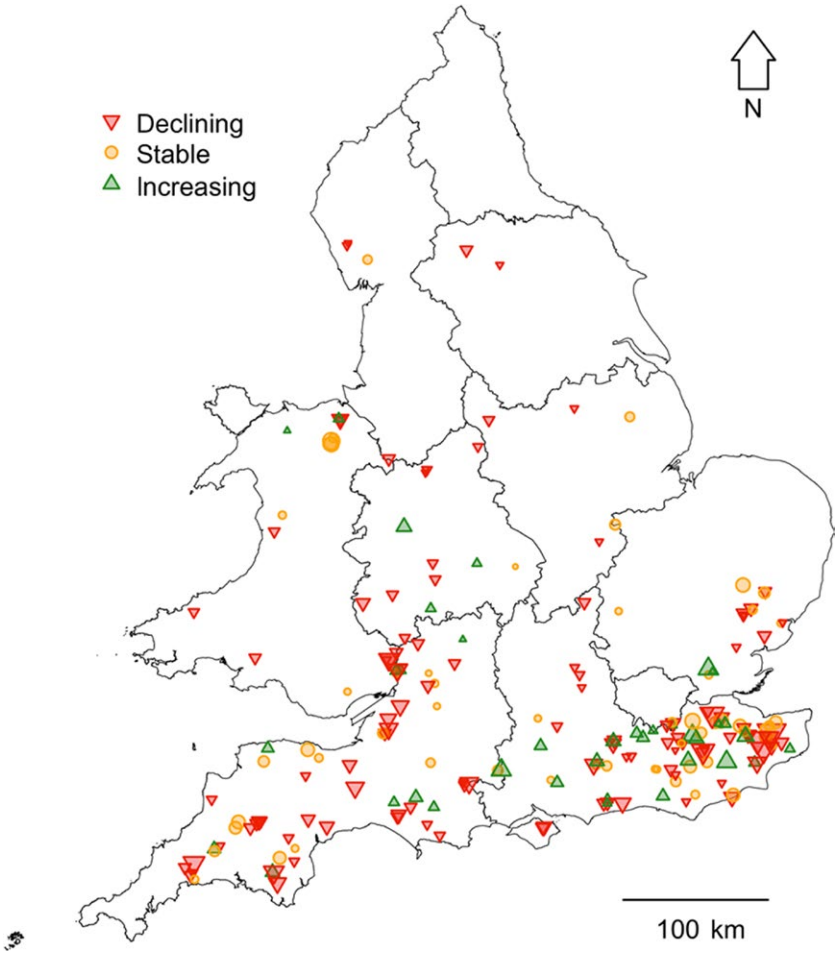

Fig. 1. Locations of 215 National Dormouse Monitoring Programme sites in England and Wales and their dormouse Abundance and Trend Indices, 1993–2014. Shape and colour indicate whether the site population is increasing (Trend Index > 0.05), stable (Trend Index of between –0.05 and 0.05), or declining (Trend Index <–0.05). The size of points is scaled by the log-transformed dormouse Abundance Index and thus is a relative indicator of population size; small populations (<3 individuals per 100 nest boxes) are all represented by the smallest size point to aid visual interpretation. The European Union regions are also shown: South-west, West Midlands, Wales, South-East, East Midlands, East, Greater London, North-East, North-West, and Yorkshire and the Humber. [Colour figure can be viewed at wileyonlinelibrary.com]

Indices in both the proximity model and the location model were greater on sites where woodland management was conducted (Figs 2 and 3a). Greater dormouse abundance was associated with greater reported abundances of honeysuckle and yew in the proximity model and with greater abundance of birch and of shrub habitats in the location model. Greater abundance of conifer trees was associated with lower dormouse Abundance Indices in both proximity and location models. In the proximity model, more woodland in the surrounding area was associated with higher dormouse Abundance Indices, whereas in the location model, sites with more woodland edges (>25 m from other woodland) had lower dormouse Abundance Indices.

At a national scale (in the proximity model), variation in dormouse Breeding Indices was also negatively related to climate PC1 (Fig. 4), indicating that dormice had more litters on warmer, sunnier sites. Location explained 19% of variance in dormouse Breeding Indices, whereas 27% could be attributed to habitat and management factors. Site-level climatic variation explained only 1% of variance in Breeding Indices and, when controlling for the location of sites, local climatic factors did not significantly affect dormouse Breeding Indices. Dormouse Breeding Indices in the proximity model, but not in the location model, were greater on sites in which more woodland management was conducted (Figs 4 and 3b). Greater dormouse Breeding Indices were associated with greater reported abundance of hazel in the proximity model and of willow in the location model. Greater abundances of conifer trees and sycamore were associated with lower dormouse Breeding

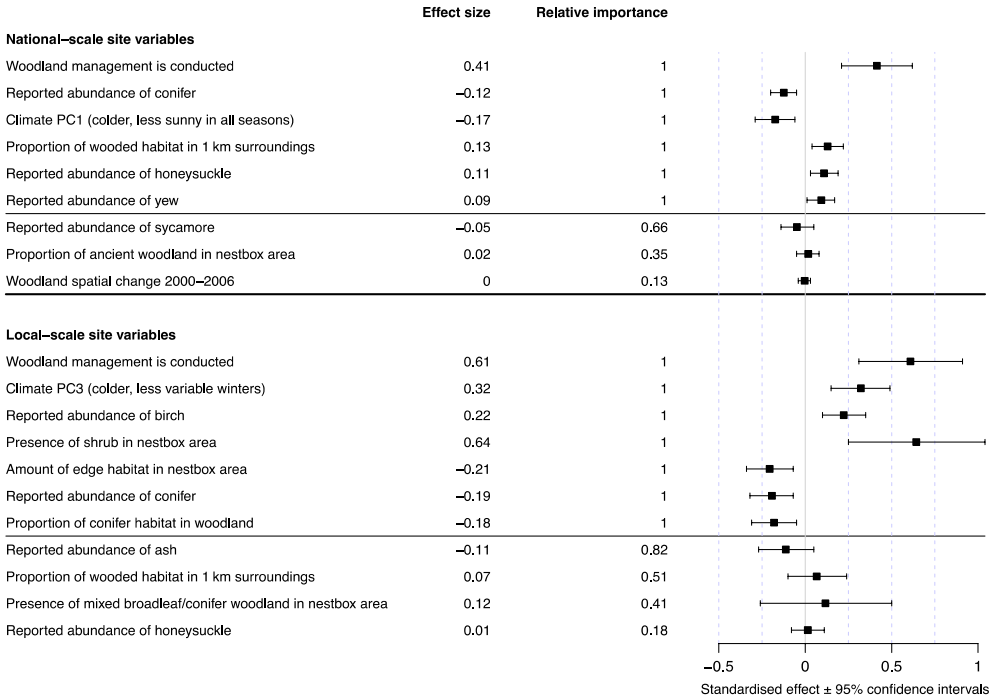

Fig. 2. Relationships between climate, landscape, habitat, and woodland management variables and dormouse Abundance Indices on 180 sites in the National Dormouse Monitoring Programme, 1993–2014. National-scale effects are from the 'proximity model' and local-scale effects are from the 'location model'. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance in the top model set are shown. 'Reported abundance' of plant species is derived from questionnaire data. [Colour figure can be viewed at wileyonlinelibrary.com]

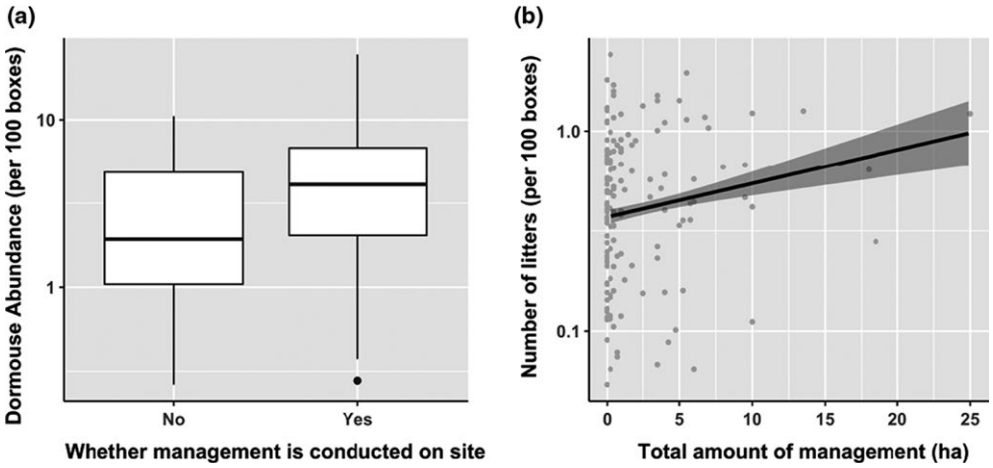

Fig. 3. Relationships between dormouse population indices and important woodland management variables. a) Dormouse Abundance Indices, in box and whisker plots showing the median (central line), inter-quartile range (box), whiskers (minimum and maximum values), of sites where management is and is not conducted; one outlier datum for a woodland where management is conducted is shown as a single point. b) Dormouse Breeding Indices of sites with different areas under annual management (based on predictions from the national scale proximity model without Indices weighting in order to aid visualisation, the effect of the amount of management in analyses was similar). Grey bands surrounding main effect lines illustrate the estimated standard error of the effect. Y axes of plots a and b are on a logarithmic scale.

Indices in both models, though the presence of mixed broadleaf or conifer habitat was positively associated with dormouse Breeding Indices (Fig. 4). In the location model, sites with lower vegetation diversity and more woodland in the surrounding area were associated with higher Breeding Indices (Fig. 4).

Climate variables had no significant impact on dormouse population Trend Indices at either the national

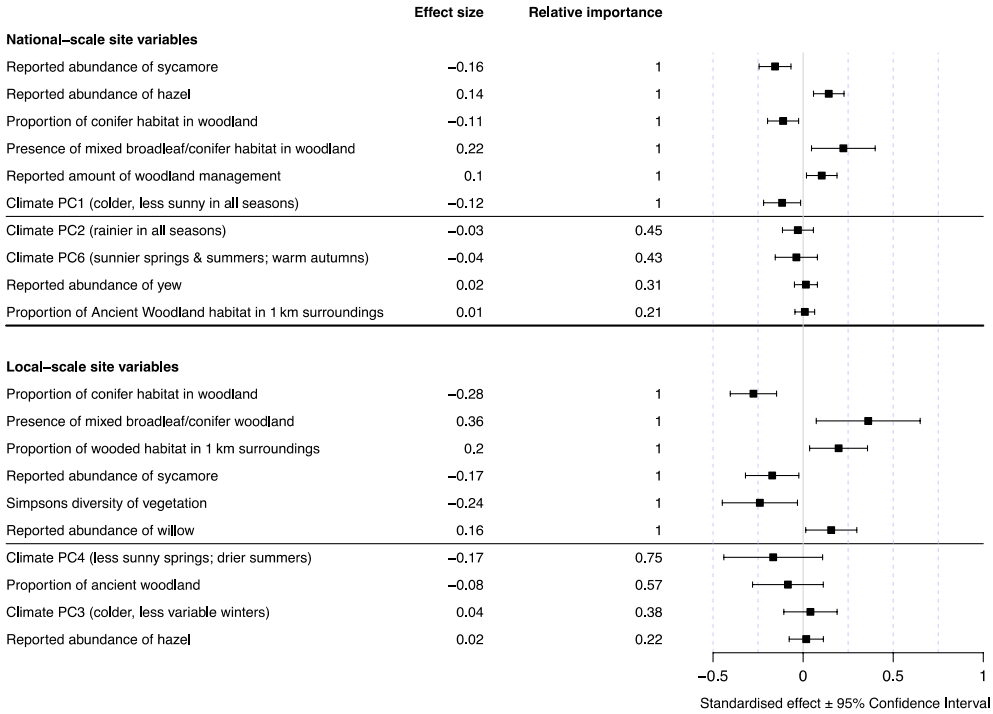

Fig. 4. Relationships between climate, landscape, habitat, and woodland management variables and dormouse Breeding Indices on 140 sites in the UK National Dormouse Monitoring Programme, 1993–2014. National-scale effects are from the 'proximity model' and local-scale effects are from the 'location model'. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance in the top model set are shown. 'Reported abundance' of plant species is derived from questionnaire data. [Colour figure can be viewed at wileyonlinelibrary.com]

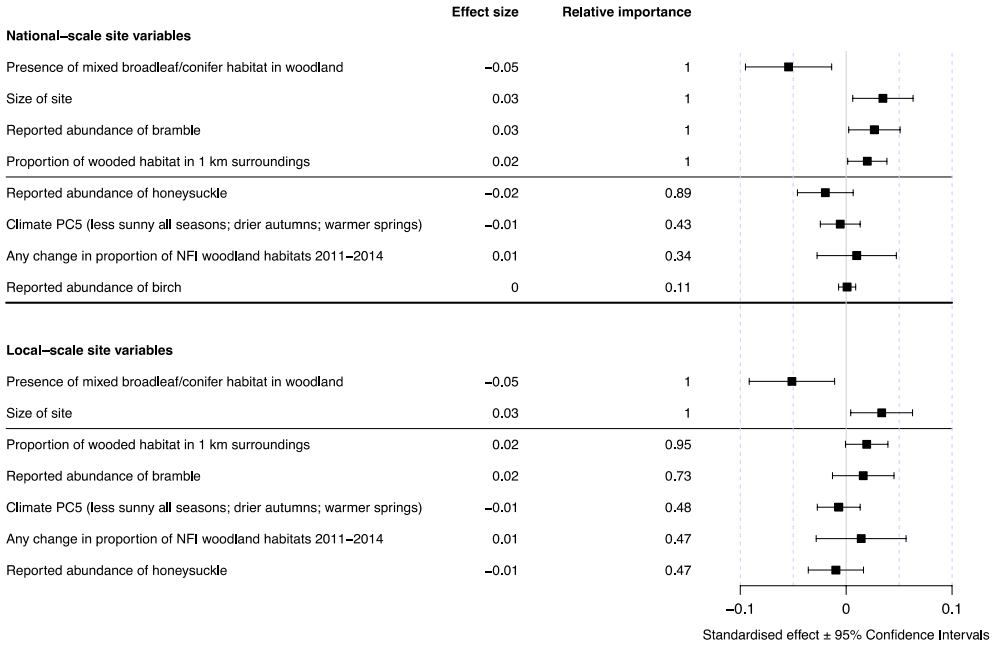

Fig. 5. Relationships between climate, landscape, habitat, and woodland management variables on dormouse population Trend Indices on 182 sites in the UK National Dormouse Monitoring Programme, 1993–2014. National-scale effects are from the 'proximity model' and local-scale effects are from the 'location model'. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance in the top model set are shown. 'Reported abundance' of plant species is derived from questionnaire data. [Colour figure can be viewed at wileyonlinelibrary.com]

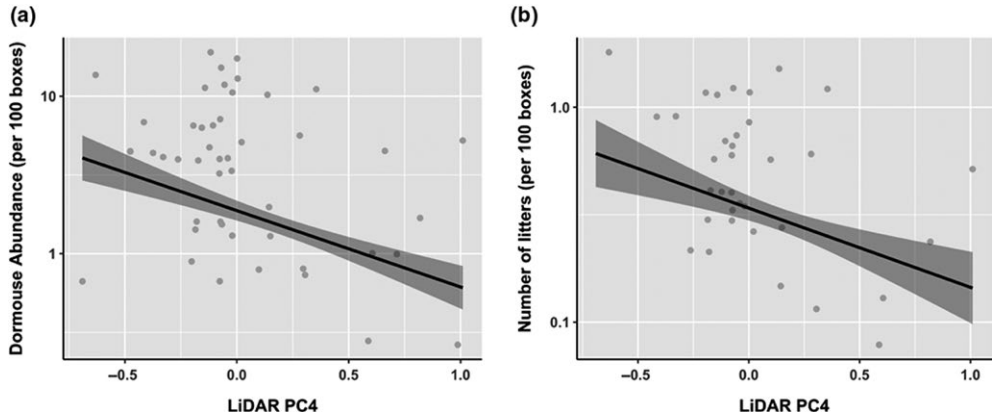

Fig. 6. Relationships between vegetation structure PC4 and a) dormouse Abundance Indices and b) Breeding Indices. Vegetation structure is described by Principal Component Analysis of LiDAR data. Grey bands surrounding main effect lines illustrate the estimated standard error of the effect.

scale (proximity model) or the local scale (location model; Fig. 5). Location was less influential in population trends, explaining only 3% of variance in Trend Indices, whereas local climate explained 1% of variance, and habitat and management factors a further 9%. Dormouse population Trend Indices in proximity and location models were higher (more positive) on larger sites and lower (more negative) on sites with greater abundance of mixed broadleaf or conifer habitat (Fig. 5). Higher Trend Indices were associated with greater reported abundance of bramble *Rubus fruticosus* and with more woodland habitat in the surrounding area in the proximity model (Fig. 5).

Vegetation structure and dormouse populations

Abundance and Breeding Indices were significantly and negatively related to LiDAR PC 4 (Fig. 6). Dormice were therefore more abundant and had more litters on sites characterised by a high proportion of vegetation that was 5 to 10 m tall, less high forest, less vegetation of 1 to 2 m tall, and less variation in canopy density. Dormouse population Trend Indices were not associated with any LiDAR PCs. Analysis of single LiDAR variables supported these results, but did not capture combinations of correlated woodland structure. Abundance Indices were significantly negatively related to the proportion of vegetation over 10 m tall (−6.48; −10.00, −2.95 95% CIs), Breeding Indices were significantly negatively related to the proportion of 2–5 m vegetation (−6.48; −10.92, −1.59 95% CIs), and Trend Indices were not related to LiDAR variables.

DISCUSSION

Our analysis of the records of a large sample of hazel dormouse monitoring sites in England and Wales indicates that some of the variance in dormouse abundance and breeding can be attributed to factors that, from a site management point of view, are intractable, e.g. location and regional and local climate. However, the influence of habitat and woodland management together outweighed the influence of climatic variation, and greater dormouse abundance and more breeding were associated with active woodland management. Thus habitat and woodland improvement at a site level hold substantial potential for improving the prospects of dormouse populations. To this end, there were site features that were associated with both greater abundance and breeding of dormice, whereas other site attributes favoured one and not the other, and so improved management might target varying requirements at different stages of the dormouse life cycle.

In relation to climate, dormice were more abundant and had more litters on sites characterised by warm and sunny springs, summers, and autumns. Locally, sites with consistently cold winters also had greater dormouse abundance, highlighting the importance of consistency in cold conditions for over-winter survival of dormice (Bright & Morris 1996).

In terms of habitat and the importance of specific plants, dormouse abundance was greater on sites with more honeysuckle, yew, and birch. While breeding was not affected by the abundance of these three species, sites with more litters, but no greater abundance, had more hazel, more willow, and less sycamore. High abundance of conifers was a negative attribute for both abundance and breeding, though where conifers were mixed with broadleaf trees, this was positive for breeding, but not abundance. In relation to landscape, dormice were more abundant and bred more on sites with more woodland in the surrounding area, and more positive trends in dormouse populations were apparent in larger woodlands.

Our study suggests that the conservation status of dormice could best be enhanced: 1) at the landscape scale,

by measures to increase woodland size and reduce fragmentation and 2) at the site scale, by implementing active management that fosters areas of shrub and successional habitats (Bonnet et al. 2016), trees and shrub habitats in the range of 5–10 m, and favours honeysuckle, yew, birch, hazel, willow, and bramble, but removes conifers and sycamore.

Dormice have been adopted as a flagship species for woodland conservation over several decades (Morris 2003). The fact that decline in dormouse populations in the UK is ongoing indicates that their conservation status is far from favourable and that pressures on populations continue to be significant (Goodwin et al. 2017). A better understanding, as provided here, of the response of dormouse populations to large-scale effects of habitat composition and management might also be used to substantiate and refine the role of the hazel dormouse as an indicator species, highlighting the various pressures on woodland environments. While many species have been shown to thrive in more mature woodland, as opposed to in the mid-successional stages preferred by dormice (Honnay et al. 1999, Russo et al. 2004), mature woodland in Europe has suffered from a general reduction in structural and species diversity and is often even-aged and lacking in understorey and edge vegetation (Honnay et al. 1999, Müllerová et al. 2015). This reduction in complexity, often as a result of declining frequency or intensity of management, has affected many taxa, including woodland birds (Fuller & Gill 2001, Quine et al. 2007, Calladine et al. 2017), butterflies (Davies et al. 2007, Broome et al. 2011, Fartmann et al. 2013), and other mammals (Ramírez & Simonetti 2011). Furthermore, the variation in woodland age and structure that we have shown to be positive for dormice can also be highly valued by people (Filyushkina et al. 2017). Thus creating better woodland habitat for dormice has the potential to increase its recreational and aesthetic value to people.

The habitats we found to be associated with favourable indices of dormouse populations have declined markedly in Europe over the last century (Hopkins & Kirby 2007, Kirby et al. 2017). At the same time, habitats associated with reduced dormouse abundance and breeding, including fragmented woodland, conifer plantation, sycamore, and high broadleaf forest, have markedly increased (Young et al. 2005, Hopkins & Kirby 2007). These changes in habitat and landscape character are attributable in large part to the loss of wooded habitats and declines in certain woodland management practices, notably coppice, and ride and glade creation (Hopkins & Kirby 2007). Localised studies have found that woodland becomes favourable for dormice one to five years following management (Capizzi et al. 2002, Juškaitis 2008), and that within these mid-successional habitats, dormouse survival is higher and condition is better (Mortelliti et al. 2014, Sozio et al. 2016).

While changes in woodland management in Europe can be attributed to many factors, such as changes in wood markets and technological changes (Quine et al. 2011), individual-level protective legislation for the hazel dormouse may also have created impediments to more favourable woodland management. The European Commission Habitats Directive (1992) and the UK Habitats Regulations (1994 and 2010) create a legal requirement to consider the risk to dormice, including to individual animals, posed by habitat alteration. This could discourage landowners from managing their woodland, to mitigate the short-term risk of accidentally killing individual dormice or destroying breeding and resting places, and may contribute to a perception that habitats must be preserved (Hull et al. 2002). Over time, this concern for individual dormice might, perhaps ironically, result in degradation of habitat quality, leading to a general failure to comply with other legal obligations, and with the overall intent of the European Commission Habitats Directive to maintain the Favourable Conservation Status of the species (Epstein et al. 2016). Other European Protected Species, such as the Siberian flying squirrel *Pteromys volans,* have been shown to have been ill-served by individual-level protection when conservation threats relate mainly to changes in habitat quality (Santangeli et al. 2013, Jokinen et al. 2015). A substantial majority of NDMP site monitors stated that conservation was the primary objective at their site. Counter-intuitively, the perception, if any, of the need for habitat preservation might therefore be most marked on sites where dormouse conservation is a key aim.

Forest management takes many forms, and the more commercial practices of larger-scale thinning and clearfell were not well represented in our sample. Larger-scale commercial clearfell could result in habitat loss, fragmentation, and population constriction and isolation (Trout et al. 2012, Bogdziewicz & Zwolak 2014). Caution should therefore be applied when generalising the positive effects of management to sites with different objectives. General principles, however, can be applied to different site types (Hartley 2002, Paillet et al. 2010), including the importance of a mosaic of tree age-classes and favoured species.

All of our sites were in woodland, and our findings in relation to habitat should therefore be interpreted in this specific context, i.e. particular features might be beneficial only when located within woodland. Dormice and many other species can thrive in mature woodland where they benefit from features such as increased numbers of tree cavities for nesting (Bright & Morris 1992). Our demonstration of the importance of successional and actively managed habitat for dormice nevertheless is valid in

widening the focus from ancient woodland habitat, which has been considered in some studies to be the principal habitat for dormice (Harris et al. 1995, Newman et al. 2003, Bailey 2007).

Greater abundance of specific plants was associated with greater dormouse abundance (honeysuckle, yew, and birch) and more breeding (hazel and willow). These plants have all been shown to be important sources of food and, in some cases, nesting material for dormice (Richards et al. 1984, Juškaitis et al. 2016). Hazel and willow may be associated with increased breeding as they provide willow inflorescences and hazel buds, flowers and catkins in spring and hazel nuts in autumn (Juškaitis & Baltrūnaitė 2013). Simpson's diversity index of vegetation on sites was, perhaps counterintuitively, negatively related to dormouse Breeding Indices, but not to Abundance Indices, at the local level. This could indicate that once abundances of beneficial species, e.g. willow, and of detrimental species, e.g. conifer and sycamore, are taken into account, diversity *per se* offers little advantage when it comes specifically to local variation in breeding. Simpson's index of vegetation was weakly positively correlated with abundances of willow and sycamore (between $r_s > 0.2$ and <0.3). This may have resulted in the Simpson's index aligning with some complex pattern of residual variation in our models of breeding.

A key habitat feature for dormice that we were not able to measure is the understorey layer (Bright & Morris 1990, Juškaitis et al. 2013). LiDAR is usually used to detect only the canopy layer, and there is currently a paucity of publicly available data on horizontal woodland structure in the UK. There are promising developments in this field, however, with the introduction of new technologies such as terrestrial radar scanning (Eichhorn et al. 2017) and waveform LiDAR (Anderson et al. 2015). Further studies on the influence of understorey layers will be beneficial, as the data and technology become more available.

The influence of climatic features was more pronounced in this study than in other work on dormouse site occupancy in continental Europe (Mortelliti et al. 2014, Becker & Encarnação 2015). This is most likely due to the greater significance of climatic variation at the latitudinal range edge of any species, which has previously been linked to the restricted distribution of the species in Britain (Bright & Morris 1996). The main axis of climatic variation among these dormouse sites (PC1) varied regionally and comprised differences in temperature and sunshine hours, which markedly influenced dormouse abundance and breeding. The influence of temperature on dormouse distribution has similarly been reported by Bright et al. (1994). Warmer, sunnier weather aids the flowering and ripening of fruits, and extends the activity period of dormice, allowing for greater foraging opportunities (Bright 1996, Bright & Morris 1996). When controlling for regional climatic effects, we found that dormice were less abundant on sites with local climates characterised by warmer, more variable winter temperatures (PC3). This accords with such weather patterns reducing hibernation survival, and ultimately population abundance (Bright & Morris 1996). Climate projections of milder, wetter winters therefore highlight the possibility of detrimental impacts on dormouse populations in England and Wales and possibly elsewhere in future (Jenkins et al. 2009).

In our previous appraisal of the volunteer-collected data from the NDMP, we found no major sampling errors intrinsic to the survey methodology (Goodwin et al. 2017). That is not to say that such citizen science surveys are without their shortcomings; data can be somewhat sporadic and tend not to be collected under rigid sampling regimes. In this analysis, we aimed to increase the reliability of our findings by only including sites surveyed for at least 5 years, which have been shown to give a reliable index of population size (Juškaitis 2006, Mills et al. 2016), and by weighting our site indices in statistical analyses, to take into account their accuracy. Some potential survey biases nevertheless remain, as sites might consistently have been surveyed in different months or at different times of day, though it is highly unlikely that survey approaches varied systematically between habitats. Another source of reported survey variation, and one which does vary highly within the NDMP, is the density of nest boxes (Juškaitis 2005), though we included nest box density in our models and found that it did not explain any more variation than the number of nest boxes (Appendix S1). As plant and management data were provided by volunteers, there may have been some element of inaccuracy in reporting, though we used broad abundance categories and very broad management classifications to reduce any effects of inconsistency. A potential problem might persist if dormouse detection probability varied between habitats. It has been suggested that nest box use by dormice decreases in summer, as shrubs, particularly brambles, grow to densities that provide good nesting habitat for dormice (Verbeylen 2012). These habitats, which would decrease apparent abundance relative to actual abundance, were in fact associated with higher dormouse abundance, breeding, and more positive trends in our models. Shrub, honeysuckle, and bramble, which are all preferred dormouse nesting habitats (Hurrell & McIntosh 1984, Bright & Morris 1992, Berg & Berg 1998), had positive associations with Abundance, Breeding, and Trend Indices. Use of nest boxes by dormice may also be lower in woodland with a high abundance of natural tree cavities (Bright & Morris 1991, 1992). However, plantation conifers tend to have very few natural cavities

(Bunnell 2013), and thus the lower dormouse Abundance Indices we observed in this habitat are unlikely to arise from this bias. The association between reduced breeding and higher abundance of sycamore, however, might indeed be confounded by this detection bias. Higher temperatures have also been found to reduce the probability of nest box use (Mortelliti et al. 2014), but we found higher abundances associated with higher temperatures. Consequently, rather than producing spurious habitat effects, any detection biases might mean our estimates of the substantial associations of dormouse indices with climate and habitat factors may be underestimates.

Despite the high profile of the hazel dormouse in Britain and its adoption as a flagship species for woodland conservation, populations have continued to decline over the last 25 years (Goodwin et al. 2017). The attributes of sites exhibiting favourable population status coincide with woodland habitats that have been in decline in Britain over the last century. Changes in woodland management practices have been integral to this decline, and we have illustrated that management is an important determinant of dormouse conservation status. Furthermore, large-scale evaluation of the effects in practice of variation in the timing, frequency, and intensity of woodland management would be beneficial in refining conservation recommendations and optimising these, alongside the wider objectives of woodland management. Further studies on the demographic drivers, such as the movement and survival of individual dormice between habitats, would also help to build a more comprehensive picture of effective management (Harris et al. 2015). A long-term effort to foster woodland protection at the landscape scale with immediate implementation of more active woodland management at the site scale is required to counter dormouse population declines and to aid their recovery as an important feature of woodland biodiversity.

ACKNOWLEDGEMENTS

We thank the dormouse monitors who collect the data for the NDMP, and to the People's Trust for Endangered Species (PTES) for their provision of NDMP dormouse population data and questionnaire data on site habitat and management. We thank Pat Morris for his advice on the manuscript. We also thank the UK Met Office and UK Climate Projections (UKCP09), the Forestry Commission; the Centre for Ecology & Hydrology, the European Commission Joint Research Centre, the Environment Agency and Natural England for data access. This work was funded by a research studentship supported by the Forestry Commission and the National Environment Research Council, and by a grant provided by PTES. Due to the confidential nature of some of the research materials supporting this publication not all of the data can be made accessible to other researchers. For more information please contact Robbie McDonald e-mail r.mcdonald@exeter.ac.uk.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supplementary Methods.